

DIFFERENCES OF PRIMARY AND SECONDARY
TERRA FIRME FORESTS ALONG THE
UAICURAPA RIVER NEAR PARINTINS,
AM ACCORDING TO THE RELATIONSHIP
BETWEEN INDIVIDUAL TREE SIZE AND VESSEL
AREA IN STEM CROSS SECTIONS

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ABSTRACT - Forest inventory and stem disk sampling were carried out in a primary forest (FP), 20 year-old and 8 year-old secondary forests (C20, C8) on a terra firme site along the Uaicurapa River near Parintins, AM. The relationship between individual tree size and vessel area (%) in stem cross sections was investigated. The number of species and individuals was 68 and 253 in the FP (/2500 m²), 23 and 45 in the C20 (/100 m²), 18 and 102 in the C8 (/100 m²), respectively. Species richness recovered along with time following abandonment, but only two species occurred commonly. The average tree height was 4.10 m in the C8 and 12.99 m in the FP. It was estimated from the standard deviation (C8: ± 1.82 m, FP: ± 7.15 m) that the development of strata had occurred with the passage of time. The aboveground biomass also differed greatly between the two stands (C8: 1.60 t/ha, FP: 259.59 t/ha). Most species showed a diffuse vessel arrangement. The vessel area (%) of tall trees tended to be high in contrast to small individuals. This means that the percentage of vessels conveying the sap vertically is dependent on tree height. Further, the vessel area of the juvenile forest was larger than that of primary forest even under comparable tree heights. It is believed that the low and uniform tree height with limited light stress causes the rapid growth rate in juvenile secondary forests.

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KEY WORDS: Primary forest, Secondary forest, Strata, Tree height, Vessel area.

RESUMO - O inventário florestal e a coleta das amostras dos cortes transversais dos troncos foram feitas em uma floresta primária (FP), e em uma floresta secundária de 20 e 8 anos (C20, C8) em terra firme ao longo do Rio Uaicupura perto de Parintins, AM, para investigar a relação individual entre o tamanho da árvore e a área de vaso (%) nas secções de cortes transversais dos troncos. O número de espécies e indivíduos foram 68 e 253 em FP (/2500 m²), 23 e 45 em C20 (/100 m²), e 18 e 102 em C8 (/100 m²), respectivamente. Apesar de muitas espécies terem sido recuperadas com tempo devido apos ao abandono, somente duas espécies aparecem comumente. A média de altura das árvores é de 4.10 m em C8 e 12.99 m em FP. Baseado no desvio-padrão (C8: ± 1.82 m, FP ± 7.15 m) foi estimado que o desenvolvimento dos estratos ocorreu devidamente com o tempo. A biomassa também difere bastante entre as duas parcelas (C8: 1.60 t/ha, FP: 259.59 t/ha). A forma de distribuição da maioria das espécies apresentou um arranjo difuso. Houve uma tendência para que a área de vaso (%) de árvores altas fosse maior que das árvores pequenas. Isso significa que a porcentagem de vasos, os quais são responsáveis pelo transporte vertical da água, é independente da altura da árvore. Assim sendo, a área de vaso da floresta juvenil foi maior que da floresta primária, mesmo em casos de árvores com alturas similares. Acredita-se que árvores de pequeno porte e uniforme com pouca assecibilidade a luz, são responsáveis pela grande taxa de crescimento das florestas secundárias juvenis.

PALAVRAS-CHAVE: Floresta primária, Floresta secundária, Estratos, Altura da árvore, Área de vaso.

INTRODUCTION

The landscape of the Middle Amazon is characterized by the seasonal inundation forest (várzea), where plants are subjected to alternating aquatic and terrestrial phases, and by the non-flooded upland forest (terra firme). Internal migrations to the region, inhabited mainly by indigenous and part-indigenous caboclos, was triggered by the late nineteenth century rubber boom. Following the collapse of the latex-based cycle of extractivism, the emigrants who remained in

the region began the development of the várzea and adjoining terra firme. Riverine changes began to accelerate after the 1950s with jute farming, and particularly after the 1980s with the replacement of jute by cattle. During the low water season, cattle are pastured on the abundant natural grasses of the várzea. The livestock are shifted to the terra firme in the high water season, when the bottomlands are submerged (Sternberg 1998). To accommodate the increasing demands for beef by Amazonian urban centers, particularly Belém and Manaus, herds expanded and along with them the deforestation of terra firme adjoining the várzea. In the late 1990s, the speculative growth began to be tempered as a result of severe competition from other breeding areas and pasture abandonment is beginning to take place. At present, researchers are debating how regeneration occurs in such places (Fearnside 1998; Uhl *et al.* 1998).

On the other hand, traditional land use has been carried out next to the cattle ranches on the terra firme. Manioc (*Manihot esculenta* Kantze.), the main staple of local inhabitants, is cultivated along with other crops under shifting cultivation. One to two hectare plots are opened in the forest by slash-and-burn, and manioc is cultivated for two years. Then, the land is fallowed, and a new site is opened. Therefore, secondary forests with differing ages are scattered on the terra firme.

Rapid inroads into the Amazon rain forest, increasingly evident since the 1980s, are changing the trend of vegetation science. For example, evaluation of deforested areas, development of selective logging methods, and afforestation techniques, are gaining ground, as opposed to studies of species diversity and exploration of lumber resources (LBA 1997). Long-term monitoring of regeneration processes, simulation studies of optimum logging intervals, and enriched agroforestry systems are being favored (Higuchi 1994; Van Leuween *et al.* 1997).



A drawback of vegetation science and plant ecology is the absence of a perspective that investigates the processes ranging from germination, establishment, and succession to the recovery of a natural forest. Studies of plant communities generally focus on species richness and aboveground biomass. Limited attention is given to species and individuals that select their own life space following the development of strata. In the field of fluid dynamics, it is well known that the amount of fluid passing through a cylinder is proportional to the product of the fourth power of the diameter and the number of cylinders (Calkin *et al.* 1986; Tyree & Ewers 1991). For a tree, it is equivalent to the diameter of vessels and their density. Canopy species are required to absorb soil water so as to cope with the potential water gradient between the ground surface and the leaf layer (Zimmermann 1983; Fitter & Hay 1985). From comparisons of vessel areas in stem cross sections and individual tree sizes in a secondary forest at the Caxiuanã National Forest, Pará, where the development of strata had begun, Tsuchiya *et al.* (s.d.) demonstrated that the vessel area of canopy species is larger than species remaining close to the forest floor. However, the relationship has not been discussed for a primary forest where trees exist in multiple layers. Further, it has not been investigated whether the vessel area remains equivalent between the primary and secondary forests when tree sizes are equal. Therefore, the first objective in this study is to compare the vessel and tree sizes in a primary forest. Secondly, it compares the relationship between the primary and secondary forests.

MATERIALS AND METHODS

The study site is located on a terra firme site along the Uaieurapa River near Parintins, AM (Figure 1). As is true with other areas of the Middle Amazon, transhumance of cattle between várzea and terra firme, small scale logging, extraction of forest products and manioc cultivation are the main activities of local inhabitants. In March 1999,



we established quadrats in a primary forest (2500 m²) and in two secondary forests (100 m² each). Hereafter, they are called FP, C20 and C8. The forest age of FP is unknown. The landowner has never used it. The C20 is a 20 year-old secondary forest fallowed after manioc cultivation. Likewise, the C8 is an 8 year-old secondary forest.

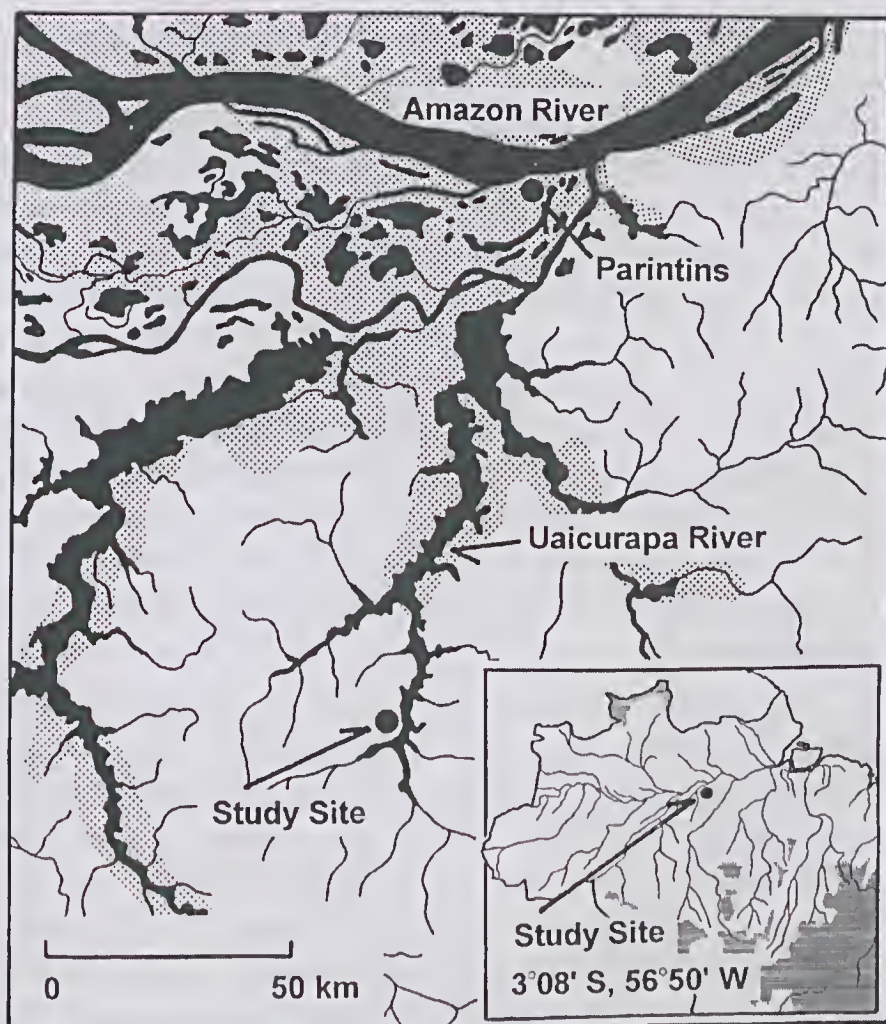


Figure 1 - Study area (Rio Uaicurapa). Rivers and lakes are shaded in black. Várzea is dotted.

Tree height, DBH and the number of stems per individual were investigated. The tree height was estimated from a distancee with a Leica-Disto and the angle of elevation with a range finder. The DBH was measured with a tape measure for individuals over 5 cm in the FP and over 1 cm in the other two stands. From these parameters, the aboveground biomass of each individual tree was estimated using allometric equations proposed by Higuehi *et al.* (1994), and the total biomass (DW: t/ha) was ealeulated (individuals of DBH<5 cm were eliminated due to the regulation). Small trees at the FP were measured separately in a sub-quadrat (100 m²) established within the large quadrat. Dead trees, fallen trees and palms were also counted but they were not included among the living trees. Species were identified from the loeal name and leaf samples were taken to the herbarium of the Museu Paraense Emílio Goeldi for identification. Stem core samples were obtained with an increment borer in the FP and C20 (height: 1 m, core length: 10 cm). In the C8, stem disks were obtained by cutting down the trees. Two samples were obtained from each individual. It was impossible to take samples from all the individuals in the quadrats. The following percentage of samples and number of speeies were covered: 37% (58 speeies) in FP, 44% (13 speeies) in C20, and 34% (15 speeies) in C8, respectively. Attention was paid to obtain samples from different tree sizes.

Growth ring measurements were conducted only with disk samples from C8. Core samples from FP and C29 were not used because it was difficult to identify the ring boundaries. Both core and disk samples were glued in a piece of wood, and were polished with a sand paper attaaehed to a grinder (Nichika, RG-A30S). Then, the 1998 tree-ring was obtained with the image analysis software (Mitani, Mae Scope 2.5) through a CCD eamera (Tokyo Denshi, CS5510) mounted on a measure scope (Nikon, MM-22). The magnification was x50 to x100. When the ring width was too large, the input was divided over several times since each input could accommodate an



area between 1.4 mm² (x100) to 6.0 mm² (x50). The area of each vessel, its number, its diameter, and circumference and brightness were measured, but we used mainly the vessel area (% of vessel area in the 1998 tree-ring) in this study. In addition, the distribution pattern of the vessel and parenchyma was also investigated.

RESULTS

Species richness, stratification, aboveground biomass at the stand level

Table 1 shows the results from the forest inventory in each stand. The number of botanical families, species and individuals appearing in all the three stands was 34, 87, 400, respectively. The FP (2500 m²) was made up of 253 individual trees (DBH=5 cm) consisting of over 31 families and 68 species. The C20 (100 m²) was represented by 45 individuals, consisting of over 15 families and 23 species. In C8 (100 m²) there were 102 individuals, with over 12 families and 18 species (DBH=1 cm). Species richness increased with time after abandonment. However, as is shown in black circles (Figure 2), the commonly appearing number of families was only 9 (Melastomataceae: N° 22, Guttiferac: N° 14, Lauraceae: N° 16, Annonaceae: N° 2, Sapindaceae: N° 30, Boraginaceae: N° 5, Apocynaceae: N° 3, Anacardiaceae: N° 1, Celastraceae: N° 8), and that of species was only 2 (*Miconia* spp.: N° 41, Maramara and *Cordia alliodora* (R. & P.) Cham.: N° 15). Species appearing frequently in the FP were *Protium heptaphyllum* (Aubl.) March. (Burseraceae, n=32), *Pithecellobium latifolium* (L.) Benth. (Leg-mimo., n=23), *Eschweilera* spp. (Lecythidaceae, n=18, Morrão). Individuals of Lauraceae (n=17) and Sapotaceae (n=16) were also large. In C8, the largest species were made up of *Miconia* spp. (n=50), *Vismia cayennensis* (Jacq.) Pers., *Vismia guianensis* Choisy, *Vismia latifolia* (Aubl.) Choisy (n=23 in total). There was no consistency both in families and species between the two stands.

Table 1 - Results of forest inventory: number of species, families and individuals, DBH (cm) and tree height (m), aboveground biomass (DW: t/ha).

Stand	Species	Families	Individuals	DBH cm	TTH m	DW t/ha
FP	68	31	253/2500 m ²	16.03	12.99	259.59
Primary forest	DBH<5 cm: not included		1012/ha	± 10.92	± 7.15	n=253
C20	23	15	45/100 m ²	8.18	7.72	112.20
20 year-old forest	DBH<1 cm: not included		4500/ha	± 6.23	± 4.33	n=30
C8	18	12	102/100 m ²	3.77	4.10	1.60
8 year-old forest	DBH<1 cm: not included		10200/ha	± 2.51	± 1.82	n=27

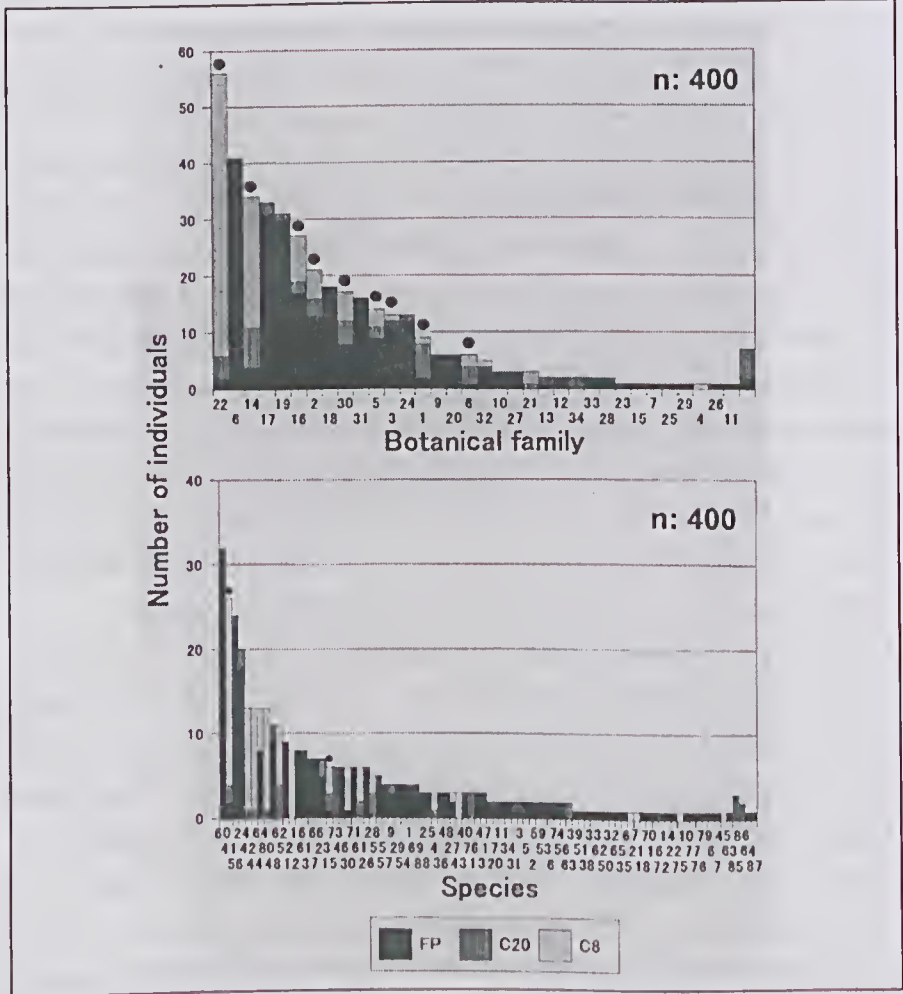


Figure 2 - Number of families (upper) and species (lower) appearing in each stand.

Except for *Astrocaryum murumuru* Mart., the dominant palm species was different between the secondary and primary forests. *Bactris maraja* Mart. and *Syagrus inajai* (Spruce) Becc. were dominant in the primary forest, but *Lepidocaryum tenue* Mart., *Cocos nucifera* L. f. and *Maximiliana maripa* (Cor. Ser.) Drude were found in the secondary forests. Also, the secondary forests were characterized by numerous vines and stumps of original trees which had re-sprouted. There was not a large difference in the number of dead trees among the stands, but the mean diameter of dead trees reached 31.4 cm in the FP and gaps were found in places.

Both tree height and DBH became greater with time, but the standard deviation also increased. In sorting them by size, the division between the large-sized individuals and the small ones becomes evident in the FP (Figure 3). Most of the trees are composed of medium and shrubby individuals lower than 20 m and 20 cm, but a small number of large-sized individuals, which form the canopy layer, pushes up the standard deviation. Plot C20 shows similar characteristics, but the stand itself remains small. The development of strata at C8 is not evident yet. Most trees are lower than 10 m in height, and the DBH is less than 10 cm. The stand is uniform and little difference is found both in tree height and DBH. The relationship between tree height and DBH is shown in Figure 4. They are not regressed by a linear function but the tree height in the FP peaks at 40m and the DBH=40 cm. There was not a large difference in the relationship of small individuals among the stands. They were distributed in the lower left of Figure 3.

The aboveground biomass (DW) estimated by allometric equations combining tree height and DBH varied greatly from 1.60 t/ha (C8) to 259.59 t/ha (FP). Although the number of individuals used in the estimate in C20 was 30 and in C8 was 27, the difference in DW attained more than 160 times, since individuals with DBH<5 cm were not



included in the calculation. The interannual change is shown in Figure 5. The horizontal axis cannot be indicated precisely because the forest age of FP is unknown. However, it is possible to observe that the DW at C20 has recovered to about one half that of FP.

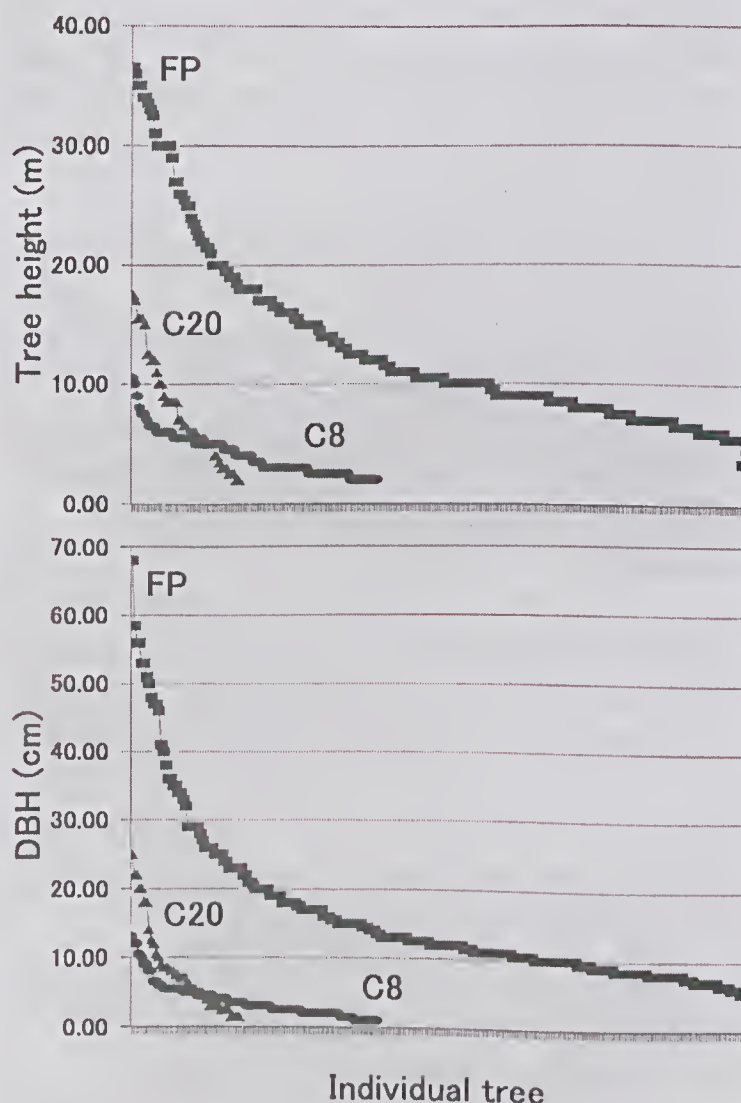


Figure 3 - Tree height (upper) and DBH (lower) of each stand sorted by size.

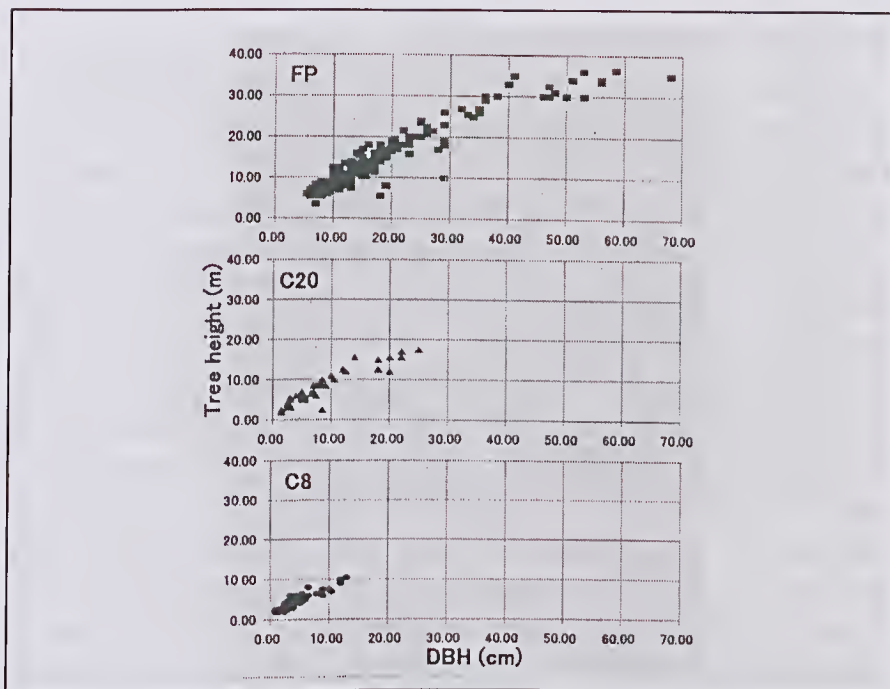


Figure 4 - Relationship between tree height and DBH.

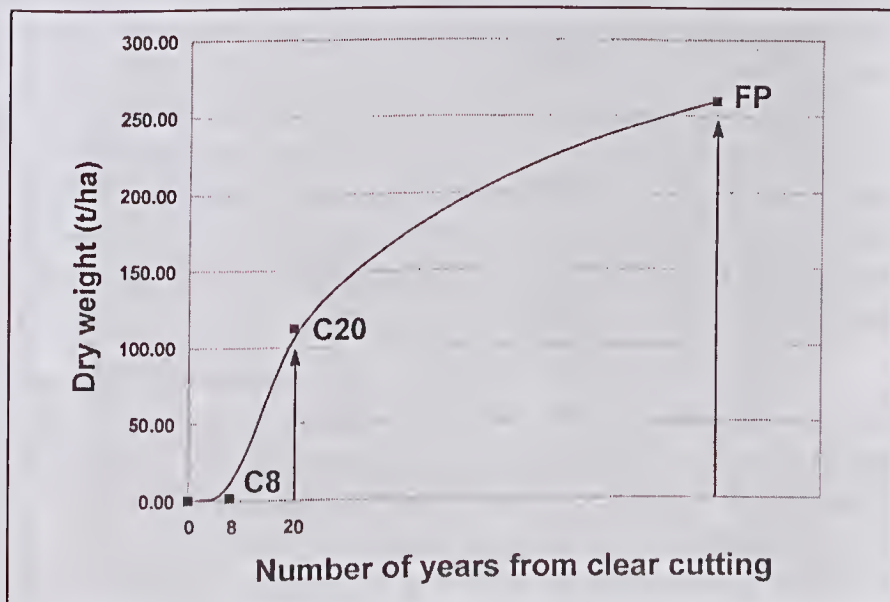


Figure 5 - Regeneration of aboveground biomass from clear cutting.

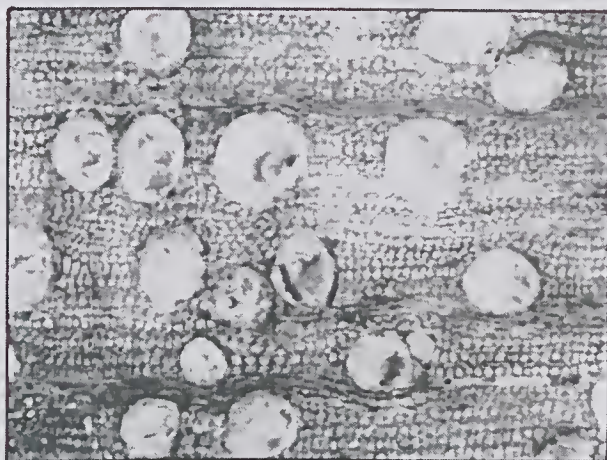
Individual tree size and vessel area

Examples of stem cross sections are shown in Figure 6. They are all 1998 growth rings, but they do not include the year's entire ring. *Trattinickia rhoifolia* Willd. at the FP (Figure 6-1, upper) is a tall tree (tree height: 35.0 m, DBH: 68.0 cm, DW: 4.8966 t) and the vessel area covers 29.69%. *Guatteria citriodora* Ducke is a small tree (tree height: 7.0 m, DBH: 8.0 cm, DW: 0.0006 t) and the vessel area reaches 3.49% (Figure 6-1, lower). In the case of C20, they are 17.0 m, 22.0 cm, 0.2526 t for *Tapirira guianensis* Aubl., and arc 4.0 m, 2.5 cm, 0.0000 t for *Cecropia jaranyana* A. Rich. (Figure 6-2). In the same way, comparable figures for *Didymopanax morototoni* Dence arc TH: 10.0 m, DBH: 12.0 cm, DW: 0.0020 t, and for *Sapindus saponaria* L. TH: 2.5 m, DBH: 3.0 cm, DW: 0.0000 t (Figure 6-3). Since some individuals had DBH less than 5 cm, they are shown with a zero DW. The vessel distribution pattern for all examples shows a diffused arrangement. Single or a few united vessels are randomly distributed in a radial pattern. One hundred thirty seven individuals, or 92% of all the individuals sampled, were diffused porous wood, and the others had the radial arrangement. There were two types of parenchyma: the vasicentric parenchyma of paratracheal type and the reticulate/banded parenchyma of apotracheal type. Parenchyma is dependent on the species, but there was a tendency that a tall tree represented the paratracheal type and a small tree the apotracheal type. Each figure illustrates two examples for each stand with different tree sizes and vessel areas. The species are different, but the vessel areas seemed to depend on the individual tree size.

Figure 7 shows the relationship between tree height and vessel area. In spite of including 58 species in the FP, the relationship was almost linear. When comparing the relationship among the three stands, it can be observed that the gradient was steeper in the juvenile forest. For example, when the tree height is 10 m, the vessel area was less than 10% in the FP, about 10% in the C20, and more than 10% in the C8.



C20

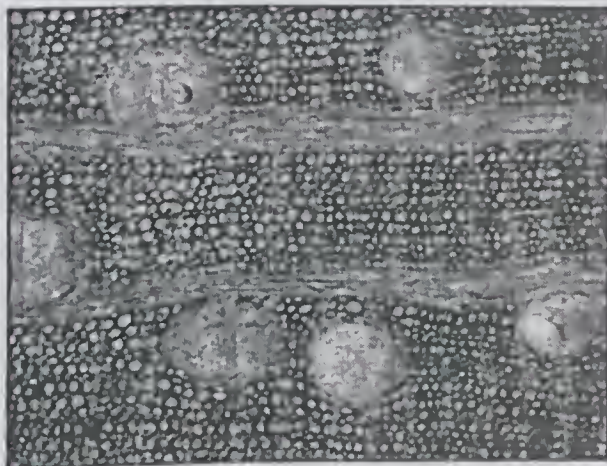


C20: No.406

Tapirira guianensis Aubl., ANACARDIACEAE

Diffuse porous wood, Paratracheal parenchyma

Vessel area: 21.60%



C20: No.380

Cecropia juranyana A. Rich., MORACEAE

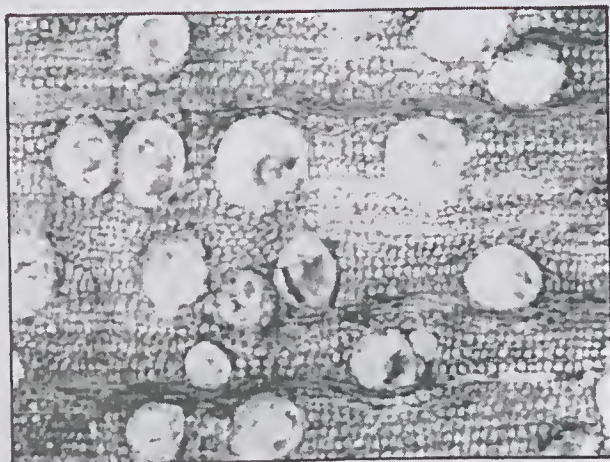
Diffuse porous wood, Apotracheal parenchyma

Vessel area: 7.98%

0 1000 μ m

Figure 6-1 - Examples of vessels in stem cross sections from each stand (elliptic tissues).

C20

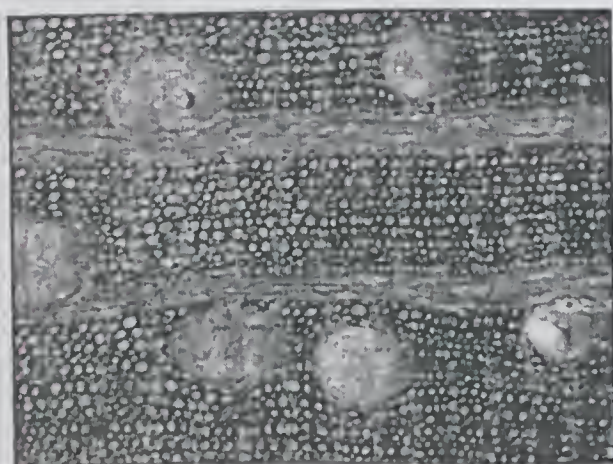


C20: No.406

Tupirira guianensis Aubl., ANACARDIACEAE

Diffuse porous wood, Paratracheal parenchyma

Vessel area: 21.60%



C20: No.380

Cecropia juranyana A. Rich., MORACEAE

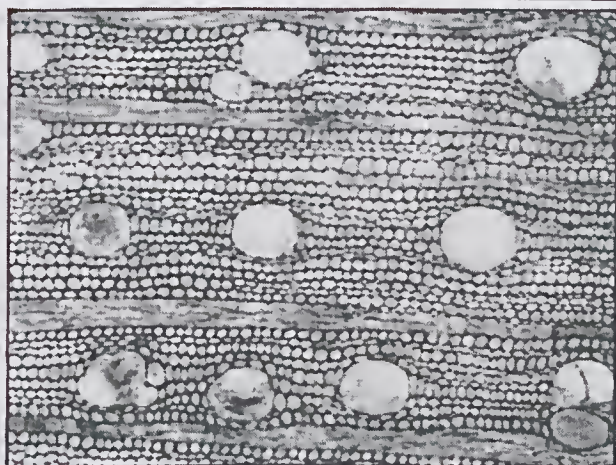
Diffuse porous wood, Apotracheal parenchyma

Vessel area: 7.98%

0 1000 μ m

Figure 6-2 - Examples of vessels in stem cross sections from each stand (elliptic tissues).

C8

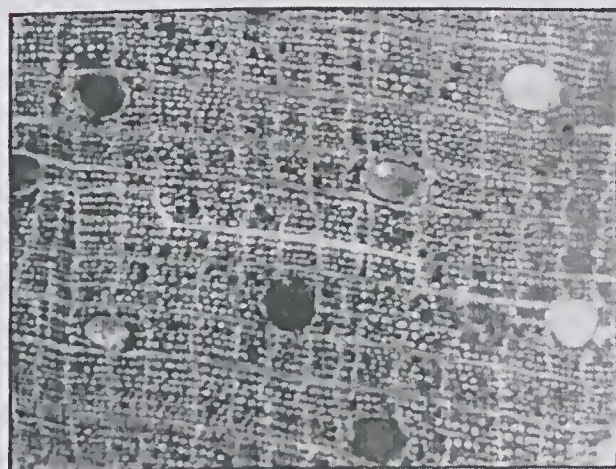


C8: No.277

Didymopanax morototoni Dence. et Planch., ARALIACEAE

Diffuse porous wood, Paratracheal parenchyma

Vessel area: 13.98%



C8: No.365

Sapindus saponaria L., SAPINDACEAE

Diffuse porous wood, Apotracheal parenchyma

Vessel area: 4.20%

0 1000 μ m

Figure 6-3 - Examples of vessels in stem cross sections from each stand (elliptic tissues).

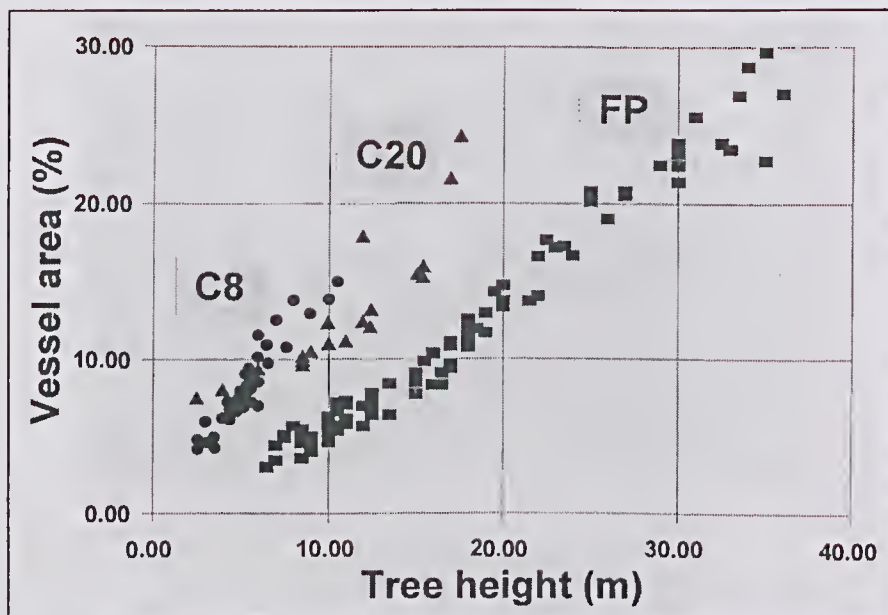


Figure 7 - Relationship between tree height and vessel area in each stand.

DISCUSSION

More than 50 forest inventories have been carried out in Amazonian primary forests (Brown *et al.* 1989). The aboveground biomass ranges between 90 and 397 t/ha, and the average is 268 t/ha. Fearnside (1987) reported a figure of 215 (± 61.7 t/ha), and Higuchi *et al.* (1994) cited 228 t/ha. The result of this study (259.59 t/ha) is close to the previously reported values. Regarding the species richness and the number of individuals, Almeida *et al.* (1993) reported that the number of families is between 31 and 47, species 84 and 196, and individuals (DBH=10 cm) 347 and 727 (/ha). It is impossible to compare the species and families because the quadrat area is different, but the number of individuals limited to DBH=10 cm at the FP (700/ha) is larger than other inventories.

All species appearing in the three stands were classified into three classes in terms of potential tree height (shrub species: <10 m, medium species: 10-20 m, canopy species: >20 m), and the number

of individuals is indicated in percentages (Table 2). The result indicated that the shrub species predominated in the C8 (74.5%), while the canopy species dominated in the FP (53.2%). This suggests that plant succession occurs continuously, and the species composition changes from shrub species to several groups of species with different heights. Thus, the change of species composition is related to the development of strata as shown in Figure 3.

Table 2 - Classification of tree species in each stand according to the potential height.

Stand	AG(%)	AM(%)	AP(%)
FP	53.2	37.0	9.8
C20	51.1	11.1	37.8
C8	23.5	2.0	74.5

AG: >20 m in tree height, AM: 10-20m, AP: <10 m

Reports refer to wood anatomy of Amazonian hardwood species, but the relationship between individual tree size and vessel parameters are not described (Sudam 1981; Loureiro *et al.* 1997). Trees must absorb water necessary for photosynthesis through vessels. The increase in vessel number and diameter bring about the increase in vessel area. This is a scheme to absorb as much water as possible against the gravity in the extension growth (Fitter & Hay 1985). Decrease in friction drag inside the vessel is accomplished by an increase in vessel diameter (Poiseuille's law: Zimmermann & Brown 1971). When the mean diameter is large, the vessel area also becomes larger, even if the number of vessels decreases. Long distance and large quantity transportation of sap is realized by this mechanism (Figure 7). However, the extension growth is not unlimited. After a given height thickening growth comes to surpass extension growth due to the potential water gradient (Figure 4). Although a high correlation coefficient exists between the vessel area and DBH, it is

a secondary product resulting from the close relationship that exists between tree height and DBH. Thickening growth, which is a horizontal growth, has no connection with vertical water potential.

In a stratified forest, e.g., primary forest, small individuals are light stressed, while in a juvenile secondary forest tree size is uniform and annual growth is large. In measuring the annual ring width of 35 stem disks obtained in C8, the tree age was found to be 6.36 and the mean radius to be 36.241 mm (Figure 8). As diameter is twice the radius, the annual growth is 11.389 mm. The average tree height of these individuals was 5.67 m, while extension growth averaged 0.89 m. As most core samples did not reach the pith, and their tree-ring boundaries could not be identified precisely, it is not possible to compare the primary and secondary forests directly. However, it is unlikely that primary forest shrubs have the same growth rate as those in the secondary forest. Not only shrubs but also canopy individuals cannot attain annual extension growth comparable to those of secondary forests. Similarly, the 1998 tree ring width from the FP is 1.850 mm (S.D.: ± 0.467 mm). This is less than one sixth of C8. Consequently, it is concluded that trees in a juvenile secondary forest with uniform forest structure can grow fast, and this fact makes the vessel area increase to support the growth.

In this study, the comparison of individual tree sizes and vessel areas from three stands with different ages indicates that the extension growth is dependent on the vessel area. However, extension growth varies between primary and secondary forests due to differences in forest structure. As a future project, we plan to measure the photosynthetically active radiation and conduct image analysis of the stomata aperture of leaves in primary and secondary forests.



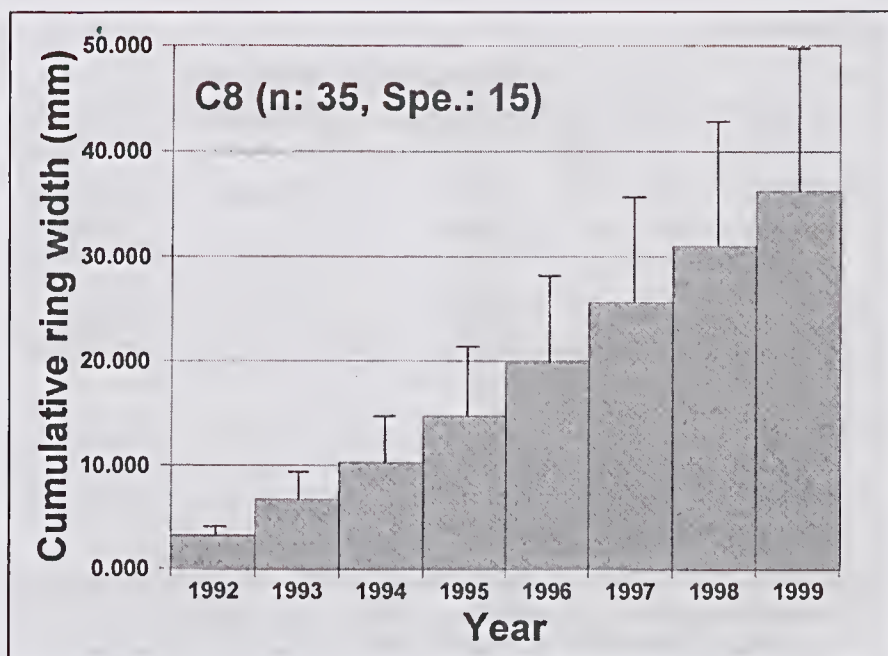


Figure 8 - Annual change in cumulative ring widths of 35 stem disks from the C8.

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